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Paleoecology and paleoenvironments of Podocarp trees in the Ameghino Petrified forest (Golfo San Jorge Basin, Patagonia, Argentina): Constraints for Early Paleogene paleoclimate

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ABSTRACT

During the Early Paleocene (Danian), Central Patagonia had a warm-temperate climate and was dominated by evergreen coniferous forests. Abundant permineralized conifer woods along with some dicot and palm leaf compressions were found in the Ameghino Petrified Forest, and provide evidence of this type of flora. All the permineralized wood and large trunks recovered were assigned to the species *Podocarpoxylon mazzonii*. An estimated tree height of 17-29m was calculated on the basis of diameter measurements. Based on 14 ring sequences, with a total of 169 rings, the mean ring width and Mean Sensitivity (MS) were 1.23 and 0.19mm respectively. The growth rings are moderately wide, extremely uniform and complacent, indicating that the environment was favourable and constant, and lacked significant stress factors limiting tree growth. Following the quantitative analysis for conifers outlined by Falcon-Lang, the growth ring anatomy of the *Podocarpoxylon mazzonii* suggests that these trees had an evergreen habit. The combination of the fossil flora, growth ring, and sedimentological analyses suggest that this mostly evergreen coniferous forest developed under warm-temperate conditions and without limiting factors.

KEYWORDS | **Early Paleocene. Petrified woods. *Podocarpoxylon*. Paleoecology. Patagonia. Argentina.**

INTRODUCTION

The relatively stable Paleocene, which followed the mass extinction events that occurred at the end of the Cretaceous known as the K-T boundary, was terminated by sudden global warming during the Paleocene-Eocene transition, known as the Late Paleocene Thermal Maximum (LPTM) and the Early Eocene Climatic Optimum (EECO) (Zachos

et al., 2001). A substantial amount of paleobotanical and paleoclimatical data from the Early Paleogene has shown that this was a period of higher global temperatures, with a global mean annual temperature of about 21°C (Wilf, 2000), 6°C higher than average temperatures today. These climatic conditions were marked by the worldwide development of tropical, subtropical and deciduous forests, as well as ice-free polar regions (Scotese, 2003). During this time, forests dominated mainly by deciduous or evergreen conifers and deciduous or evergreen broad-leaved dicots grew at high latitudes (Behrensmeyer et al., 1992 and references therein).

Detailed knowledge of the South American paleoflora plays an important role in understanding the ecosystem diversity, climate and paleoecology that existed in the mid-latitude Southern Hemisphere during the Early Paleocene. Fossil floral assemblages from 46°S in Patagonia have demonstrated the existence of diverse ecosystems including tropical rain forests, montane rain forests, mangrove communities, swamp forests, savannas and sclerophyllous forests (Petriella, 1972; Romero, 1986). A macrofloral assemblage from 45°S has recently confirmed that these floral communities were more diverse than their North American analogs (Iglesias et al., 2007).

In this paper we describe a paleobotanical and sedimentological study of the Early Paleocene flora from the Ameghino Petrified Forest, Patagonia, Argentina, located in the province of Chubut (Fig. 1). This site is found in the southern area of the North Patagonic Massif, near the northern edge of the San Jorge Basin, in sediments of the Salamanca Formation. Few previous geological and sedimentological contributions have been focused upon the Ameghino site (Aliotta et al., 1977; Rodríguez and Panza, 2003). The permineralized macrofossil flora has never before been studied, and previous works on other permineralized macrofloral assemblages from the Early Paleogene in Patagonia are also scarce (Conwentz, 1885; Kraüsel, 1924; Boureau and Salard, 1960; Salard, 1961; Romero, 1968; Petriella, 1972; Ragonese, 1980; Nishida, 1984a,b; Nishida et al., 1988, 1989; Brea, 1995; Matheos et al., 2001; Brea et al., 2005a,b; Brea and Zucol, 2006; Terada et al., 2006; Herbst et al., 2007).

Other paleobotanical records from the Salamanca Formation are important, having revealed a rich flora of gymnosperms, angiosperms, and ferns that were, preserved in the form of palynomorphs, phytoliths, leaf compressions, and petrified woods (Berry, 1937; Archangelsky, 1973, 1976; Archangelsky and Romero, 1973; Archangelsky and Zamaloa, 1986; Martínez, 1992; Somoza et al., 1995; Ruiz et al., 1999; Bellosi et al., 2000; Zamuner et al., 2000; Matheos et al., 2001, 2006; Brea et al., 2005a, b; Iglesias, 2007; Iglesias et al., 2007; Zucol et al., 2004, 2008). Early Paleocene floras have also been described from Bororó Formation (Scafati et al., 2009 and reference therein) and the Río Chico Group in the Golfo San Jorge Basin (Brea and Zucol, 2006; Brea et al., 2009; Raigemborn et al., 2009).

This study's focus is a description of the Ameghino Petrified Forest's permineralized wood assemblages, including growth-ring analysis and paleoecological interpretation, in order to reconstruct the area's paleocommunity and allow comparison with other Paleocene forest paleocommunities.

This report is a contribution to our knowledge of Paleogene paleobiotic environments and provides new evidence regarding the existence of Early Paleocene subtropical evergreen forests at mid-latitude in Southern Hemisphere.

GEOLOGICAL SETTING AND STRATIGRAPHY

Paleontological and geological studies of the Salamanca Formation have assigned this unit to the Early Paleocene,

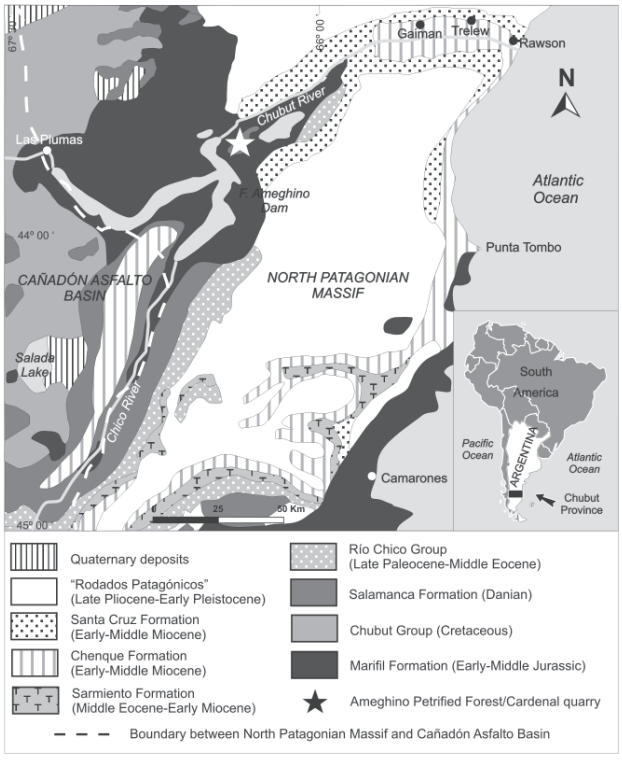

FIGURE 1 | **Geological sketch of the study area (modified from Ardolino et al., 2004) located in the northeast of Chubut province, neighbouring the Northpatagonic Massif (Hervé et al., 2008) and the Cañadón Asfalto Basin (Cortiñas, 1996). The star shows the location of the Ameghino Petrified Forest.**

mainly on the basis of foraminifera and ostracods that are directly related to the Danian stage (Feruglio, 1949; Bertels, 1964, 1973; Méndez, 1966; Camacho, 1967; Chebli and Serraiotto, 1974; Andreis, 1977). Recently updated stratigraphic ages and radiometric dates for this Formation (Iglesias, 2007; Iglesias et al., 2007) indicate an age-range between the foraminiferal zone P1c (Upper Danian) and the Danian-Selandian boundary (61.7 ± 0.2Ma).

The Ameghino Petrified Forest is located in the lower section of the Salamanca Formation. Paleontological and geological studies have assigned this unit to the Early Paleocene. The largest outcrop is found at the Cardenal limestone quarry in the lower valley of the Chubut River (43° 33' 12'' S and 66° 15' 58'' W) (Fig. 1). This outcrop is approximately 30m thick and consists of clastic and carbonatic sediments related to a transgressive marine. This sedimentary succession lies unconformably upon the Marifil Formation (Early-Middle Jurassic) and it is overlain by tuffs and fine ashes of the Middle Eocene-Early Miocene Sarmiento Formation (Fig. 2).

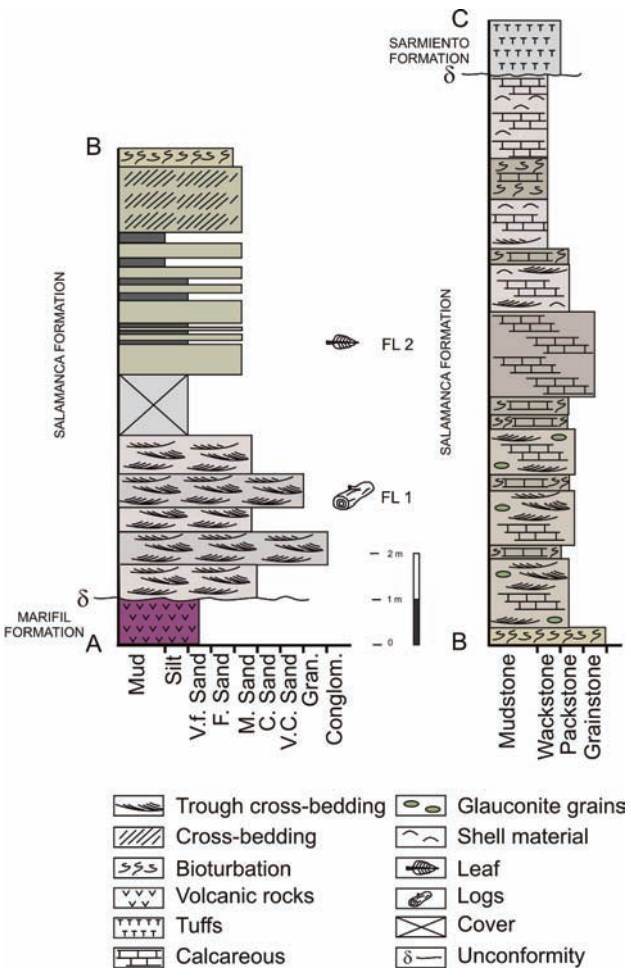

FIGURE 2 | **Lithostratigraphic section of Salamanca Formation at Ameghino Petrified Forest locality. A-B) Lower section, B-C) Upper section.**

In this area, two sections of the Salamanca Formation have been recognized (Rodríguez and Panza, 2003). The lower section (12m thick) is integrated with silicoclastic materials showing important lateral facies variations that are related to an estuary or bay with initial fluvial infilling.

This section is mainly composed of medium-brown to grey pebbly sandstone with sporadic pebbly layers, abundant quartz and lithic fragments and mainly volcanic clasts. Bodies are lenticular in shape and 1–3m thick, and the main sedimentary structures have planar, cross and graded bedding. At the base of the profile, in very coarse sandstones, the fossiliferous level I (FL 1) contains exclusively large pieces of permineralized woods and stumps (Figs. 2 and 3).

Fourteen anatomically preserved stems between 6.70 and 12.80m in exposed length, and with an average diameter of 40cm, were found in this lower section of the Salamanca Formation (Fig. 3).

In the center part of this section fine heterolithic facies integrated with claystones and fine-to-medium sandstones dominate the sequence. These are overlain by medium sandstone bodies where cross-bedding is the characteristic structure. The section is terminated by a bioturbated sandstone bed. The fossiliferous level II (FL 2), located at 11.50m above the base of the profile in heterolithic facies contains palm and dicot leaf compressions with fewer wood fragments (Fig. 4).

Toward the upper part of this unit, carbonate sedimentation and bioturbation increase markedly with respect to the lower section. The upper section (15–18m thick) is composed predominantly of limestones (packstones and wackestones), with great lateral continuity and occasionally intervals of intense bioturbation (Fig. 2). Trace fossils in the calcareous bodies were identified as *Thalassinoides, Palaeophycus* and *Ophiomorpha* ichnogenera (Fig. 3) that are assigned to *Glossifungites* ichnofacies (Rodríguez and Panza, 2003). Plant remains were not preserved in these types of facies.

MATERIAL AND METHODS

Field studies were carried out from 1999 to 2004. The Salamanca Formation was examined in detail at the Cardenal quarry and the complete profiles were measured and described with bed-by-bed recording (Fig. 2). The trunks and wood fragments were permineralized by silicification.

The plant fossils of FL 1 were recorded with respect to their quantity, taxonomic representation, distribution,

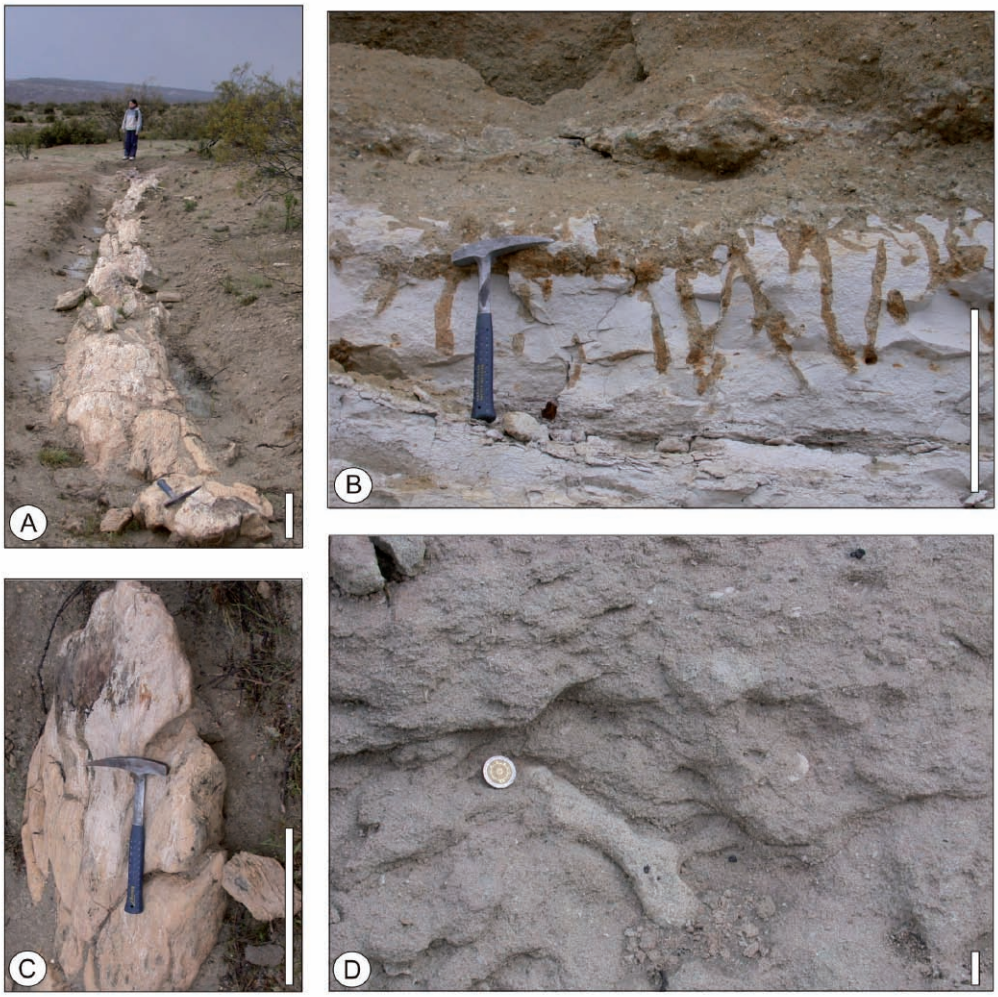

FIGURE 3 | **A) Portion of an exposed large trunk of *Podocarpoxylon mazzonii*. B) View of *Glossifungites* ichnofacies, *Thalassinoides* sp. with passive filling. Scale bar: 20cm. C) Natural view the fragment wood of *Podocarpoxylon mazzonii* at Ameghino Petrified Forests. D) *Thalossinoides* sp. in fine sands. Scale bar: 20cm in A-C; Coin scale: 2.2cm in diameter in D.**

orientation and state of preservation (Kidwell et al., 1986). These parameters allowed an estimation of their degree of transportation prior to burial, with assemblages categorized as either autochthonous, hypautochthonous, or allochthonous taphocoenoses.

The analysis of fossil forest paleoecology and paleoclimatology involved three main aspects: the taxonomic composition, the vertical distribution indicating canopy position, and the growth-ring analysis. All these aspects were also integrated with taxonomic-phenological information to infer the environmental conditions under which the community developed.

Fourteen petrified stems with good cellular preservation of secondary xylem were analyzed. Standard thin sections (cross, tangential longitudinal and radial longitudinal sections) were used to describe the woods. The terminology for this study was taken from glossaries of wood anatomy (IAWA Committee, 2004), the terminology developed for Mesozoic conifer-like woods by Philippe and Bamford (2008) and the standardized measurements established by Chattaway (1932). All fossil wood from the FL 1 level was identified as belonging to the same morphogenus and morphospecies using wood identification keys for extant woods and fossil descriptions (Greguss, 1955; Tortorelli, 1956; Bamford and Philippe, 2001; García Esteban et al., 2002, 2004).

Wood pieces with a diameter of less than 8cm were not considered because they may have represented parts of shrubs or tree branches. According to Mosbrugger (1990), a woody plant is a tree when it has a diameter of more than 7.5cm at breast height. Twelve fossil logs with completely preserved cross-sections were measured in the field in order to estimate original diameters ($D_{est.}$) using the formula proposed by Philippe et al., 2009 ($D=2R=4a/\pi \sim 1.27a$, where a is the major axis radius, see p. 87). These measurements can be used as an alternative to estimations of height (Philippe et al., 2009). Predictive models applied to extant conifers and angiosperms have allowed the formulation of the relationship between stem diameter and height (Niklas,

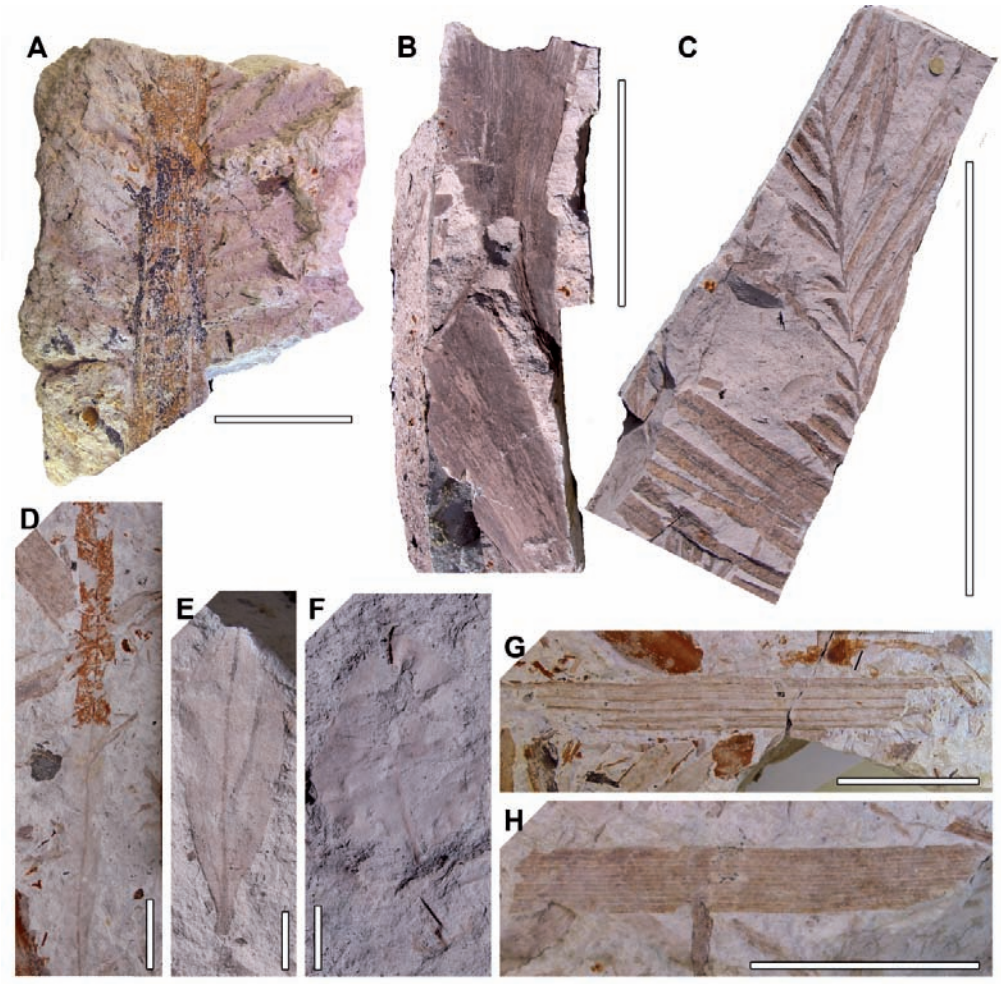

FIGURE 4 | **Leaf compressions. A) Fragment of palm leaf showing the disposition of the segments, scale bar: 5cm. B) Two bracts of palm leaves, scale bar: 30cm. C) Articulated palm leaf, scale bar: 50cm. D) Long and narrow morphotype of dicotyledoneous leaf, scale bar: 1cm. E) Elliptic narrow morphotype of dicotyledoneous leaf, scale bar: 1cm. F) Wide ovate morphotype of dicotyledoneous leaf, scale bar: 1cm. G and H) Two fragment of different segments of palm leaves, scale bar: 5cm.**

1994a). The correlation of these features can be used to reconstruct the height of fossil plants whose basal stem diameters are known or inferred (Niklas, 1994b; Philippe et al., 2009). Estimated height was calculated on the basis of diameter ratios observed in living plants using known stump diameters (Niklas, 1993, 1994a, b).

The critical buckling height (H_{crit}), or the maximum height which a vertical trunk can reach before it theoretically undergoes buckling, was estimated using Niklas' (1994a) formula: $H_{crit} = C(E/\varrho)^{1/3} D^{2/3}$, where C is the constant of proportionality (= 0.792), E is Young's modulus (958.1 x 10^6kg m^{-2}), ϱ is the bulk density of the ma-terial (tissues) used to construct the columnar stem (468.9kg m^{-3}) and D is the stem diameter. This formula eventually sim-plifies to a multiplication of $D^{2/3}$ by 95.75 (Creber and Ash, 2004; Artabe et al., 2007). The critical buckling height (H_{crit}) is the height at which the mechanical structure of the wood fails, leading to the collapse of the tree. Because trees never actually reach H_{crit}, estimated tree heights were calculated on the basis of trunk diameter-to-height ratios observed in living trees (Niklas, 1993, 1994a, b) using the formula: $H_{est} = 27.8\ D^{0.430}$, where D corresponds to fossil stump diameters (Table 1).

The Safety Factor (SF) was obtained by dividing H_{crit} by the estimated height (H_{est}) (Table 1). The SF, which can be taken as the ratio of the maximum loading likely to be experienced under the operational (normal) loadings on a structure, is typically based on the statistical probability that certain types of loading will occur (Niklas, 1992).

Growth rings of the fossil woods were also analyzed quantitatively. They were measured from thin sections and polished blocks, and then analyzed using dendrological techniques. The growth rings were measured to the nearest 0.01mm with Essex digital calipers. Statistical parameters were determined for the analysis of growth rings in gymnosperm fossil woods. Several growth ring parameters were measured: number of years, mean ring width, maximum ring width, minimum ring width, narrowest ring, widest ring, presence and number of false rings, frost rings, Mean Sensitivity (MS) and Annual Sensitivity (SA)

TABLE 1 | **Estimated height and diameter of fossil forest. Estimate original diameters (D_{est}) trunks using the Philippe' formula (Philippe et al., 2009) were used to calculate the critical bucking heights (H_{crit}), the estimated height (H_{est}) and the Safety Factors (SF) following Niklas (1993, 1994a, b)**

stump	Diameter (cm)	Estimated height (H_{est}) (m)	Critical height (H_{crit}) (m)	Safety Factor (SF)
1	83	25.66	84.67	3.3
2	66	23.25	72.78	3.13
3	72	24.14	77.09	3.19
4	67	23.4	73.51	3.14
5	45	19.72	56.53	2.87
6	64	22.94	71.32	3.11
7	46	19.91	57.35	2.88
8	43	19.34	54.86	2.84
9	40	18.75	39.36	2.4
10	50	20.63	60.6	2.94
11	40	18.75	39.36	2.4
12	140	32.13	119.56	3.72
Average	63	22.38	67.25	2.99
Maximum	140	32.13	119.56	3.72
minimum	40	18.75	39.36	2.4

(Fritts, 1976; Creber, 1977; Creber and Chaloner, 1984a, b, 1985; Francis, 1986).

Following the terminology of Falcon-Lang (2000a), the term 'ring boundary' is used here to describe the discontinuity between the late-wood cells of one ring and the earlywood cells of the following ring. The term 'ring increment' is used to describe the region between two adjacent ring boundaries, and radial diameters of individual cells across each ring increment were measured. Also following Falcon-Lang (2000a), five adjacent files of cells were measured for each ring increment and these data were averaged to create the final plots.

In this method, the cumulative algebraic sum of each cell's deviation from the mean of the radial diameter was calculated for each growth ring increment and plotted as a zero-trending curve (CSDM curve). For each ring increment, the percentage skew of the zenith of CSDM curves from the centre of the plot was also calculated. Taking into account the fact that deciduous conifers predominantly produce left-skewed or symmetrical CSDM curves, while evergreen conifers have predominantly right-skewed CSDM curves, the fossil tree's deciduous habit could be inferred. Because the percentage of latewood may be strongly influenced by leaf longevity, in addition to reflecting intensity of climate seasonality, two ring boundary aspects were quantified. This was done using the method described by Falcon-Lang (2000b) to calculate the Ring Markedness Index (RMI). First, the percentage of diminution in a ring increment was calculated using the percentage of diminution (x) = (b/a)*100; where a = maximum cell diameter and b = maximum cell diameter minus minimum cell diameter. Second, the percentage of latewood in each growth ring increment was calculated using Creber and Chaloner's (1984a) method: percentage of latewood (y) = (d/c)* 100; where d = number of cells in each ring increment and c = number of cells from the point where the CSDM curve reaches zero for the last time. The product of these two parameters was then calculated to give the Ring Markedness Index (RMI) [= (x*y)/100].

The quantitative values provided in the anatomical description below are based upon 20 measurements. The average is given first, followed by the minimum and maximum values, which are given parentheses.

The material was studied with a Nikon Eclipse E200 light microscope and the microphotographs were taken with a Nikon Coolpix S4 digital camera. Fossil samples and microscope slides were deposited at the Museo Egidio Feruglio (MEF), Trelew, Argentina, under the acronyms MPEF-Pb.

SYSTEMATIC PALEONTOLOGY

Class: Coniferopsida Gifford and Foster, 1989
Order: Coniferales Gifford and Foster, 1989
Family: Podocarpaceae Page, 1990
ORGAN GENUS *Podocarpoxylon* Gothan, 1905
Type species: *Podocarpoxylon juniperoides* Gothan, 1905
Podocarpoxylon mazzonii (Petriella, 1972) Müller-Stoll and Schultze-Motel, 1990
Figure 6 A-J

Material: MPEF-Pb 2187a-c to MPEF-Pb 2200 a-c.

Locality: Ameghino Petrified Forest, Chubut, Argentina.

Stratigraphic unit: Salamanca Formation.

Age: Early Paleocene (Danian).

Description: Pycnoxylic secondary wood with growth rings slightly demarcated and the transition from earlywood to latewood gradual, often demarcated by a few layers of thick-walled, tangentially-compressed tracheids (Fig. 5A). The range of growth ring width is 1.27mm to 2.72mm. Six to eleven rows of cell comprise the late wood. The earlywood is made up of 11 to 25 rows of tracheids.

Tracheids: Earlywood tracheids are quadrangular-rectangular with oval-shaped lumens and are thick-walled in cross section. Some areas show alteration and tracheid shapes are distorted. Late wood tracheids are flattened radially, with thick walls in cross section (Fig. 5A, D). In earlywood, the mean tangential diameter of tracheids is 57µm (45–75µm) and the mean radial diameter is 56 µm

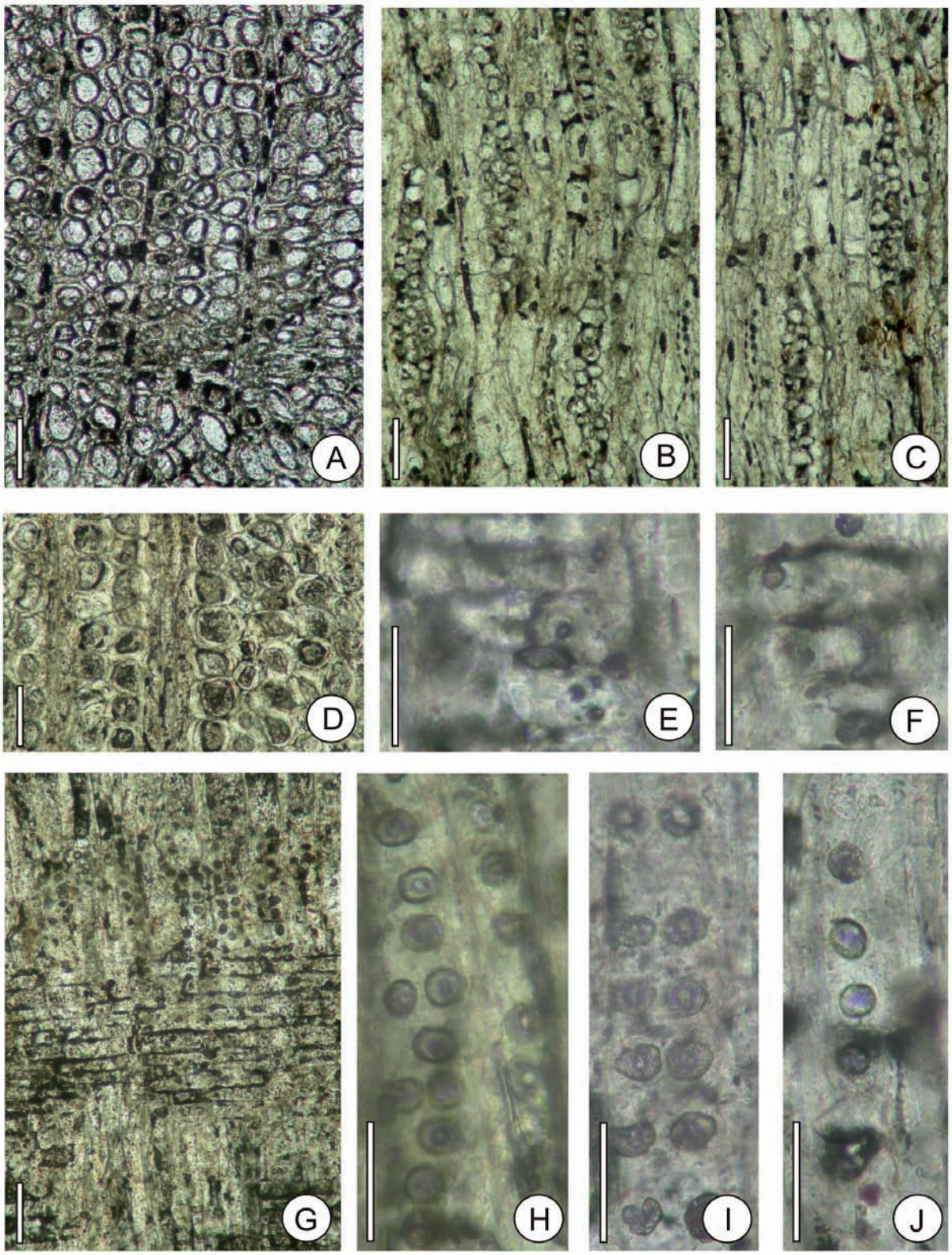

FIGURE 5 | ***Podocarpoxylon mazzonii.*** **Cross section of the wood to show growth rings. B-C) Tangential section, showing the height, width, and distribution of rays. D) Details of the tracheids and rays in cross section. E-F) Radial section, showing cross fields pits. G) Radial section to show the ray cells, and uniseriate and biseriate bordered pits on the tracheid wall. H-J) Details of uniseriate, partially biseriate and biseriate bordered pits on the radial wall of the tracheids. Note the biseriate the bordered pits are circular or oval, opposite and separate arrangement. Scale bar: 100µm in A-D, G-J; 50µm in E-F. Scale bar: 100µm in A-D, G; 50µm in E-F, H-J.**

(45–75µm). In late wood, the mean tangential diameter of tracheids is 58.75µm (45–75µm) and the mean radial diameter is 20.75µm (15–25µm).

The thickness of the double wall between two tracheids is 10.50µm (7.62–12.70µm). Tracheids arranged in regular radial rows are separated by rays. The rays are separated from each other by 2–10 rows of tracheids; with an average of 5.65 rows.

In radial section, tracheid pitting is frequently uniseriate and occasionally biseriate (Fig. 5H, I, J). The bordered pits are circular; when biseriate the bordered pits are circular or oval, opposite and have a separate arrangement (Fig. 5H, I). Pit pores are circular in outline and 12.95μm (10.16–15.24µm) in diameter. Inner apertures are circular and enclosed, with a diameter of 4.66µm (3.81–5.08µm). There are no pits on the tangential walls.

Rays: The radial system is homogeneous, comprised of oval parenchyma cells (Fig. 5G). Rays are uniseriate, occasionally biseriate and rarely triseriate (Fig. 5B, C). Rays are 53.25µm (29.40–73.50µm) wide; and low, 13 (4–24) cells high, and 222.79µm (137.2–333.2µm) in height. The mean number of rays per linear millimetre is 3.16 (2.04–5.10).

Cross-fields: Pits are of the cupressoid type, with mostly 1–2 circular pits per field, with large apertures and thin, weakly-defined borders in each pit (Fig. 5E, F).

Axial parenchyma: Diffuse. Rare parenchyma cells have smooth axial walls and smooth horizontal walls.

Comments: The structure of this fossil wood corresponds to that of *Podocarpoxylon* Gothan, 1905, which is characterized by abietinean radial pitting in the tracheids, cross-field pits mostly 1–2 per field, which are small and circular to oval, ray cells with smooth walls and scarce axial parenchyma (Del Fueyo, 1998; Bamford and Philippe, 2001; Philippe and Bamford, 2008; Gnaedinger, 2007). Based on the presence of these types of cross-field, tracheid pitting and rays, the podocarp woods from the Ameghino Petrified Forest could be included within the species *Podocarpoxylon mazzonii* (Petriella, 1972) Müller-Stoll and Schultze-Motel, 1990, which was also recorded in the Paleocene Bororó Petrified Forest in Patagonia (Petriella, 1972).

PALEOECOLOGY AND PALEOCLIMATOLOGY OF THE FOSSIL RECORD

Although in the FL 1 fossiliferous level the materials were transported, the excellent preservation of the wood and the presence of stumps suggest that these materials were transported only short distances from their growth site. Thus, they are considered hypautochthonous, living close to the coastal margin and at a date prior to the Paleocene transgression over the basin.

Trunks are characterized by preferential orientation perpendicular or oblique to the paleocurrents (Fig. 6). This could indicate that the large trunks were abundant and interfered with each other during translocation, with this interference resulting in a variety of orientations when the trunks were finally deposited (MacDonald and Jefferson, 1985).

The FL 2 fossilferous level contains leaf compressions and a scarce amount of petrified wood fragments. Identified leaf morphotypes are those two palms. One of these palms was characterized by large and pinnate leaves, while the other's leaves were palmate. Based on these leaf shapes and venation patterns, the palm leaves could be related to basal groups of the Arecaceae family (Fig. 4A, B, C, G, H). Three different dicotyledonous morphotypes were also present. All of these had large-size leaves with coriaceous texture and entire margins. The texture and architecture of these dicotyledonous leaves suggest a woody habit for their plants of origin (Fig. 4, D, E, F). The co-occurrence of palms, dicotyledonous trees and Podocarpaceae trees,

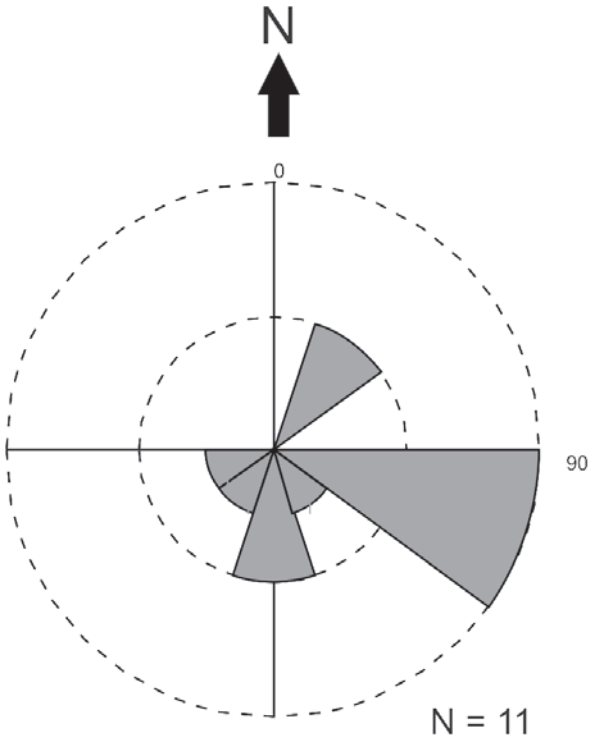

FIGURE 6 | **Rose diagram showing orientations of the longitudinal axes of the trunks in the Ameghino Petrified Forest.**

associated with *Glossifungites* ichnofacies, suggests an unusual proximal-shore paleocommunity.

In order to analyse the vertical distribution of vegetation in this paleocommunity, the estimated original diameters of trunks were used to estimate the height parameters of the trees from the Ameghino Petrified Forest, specifically the critical bucking heights (H_{crit}), the estimated height (H_{est}) and the Safety Factor (Niklas 1993, 1994a, 1994b). Table 1 summarizes these values based upon Niklas's allometric equations. *Podocarpoxylon mazzonii* was calculated to have had an average estimated tree height of 20.07m, a maximum height of 28.80m and a minimum height of 16.80m. These maximum and minimum heights correspond to stump diameters of 89.13 and 25.46cm, respectively.

Fourteen ring sequences ranging from 4 to 28 rings in length were measured for fourteen well-preserved fragments of fossil wood, with a total of 169 rings measured for the whole assemblages. These measurements indicate the existence of relatively uniform growth seasons, but with each one having a terminal event that produced a cessation or retardation in cambial activity.

Podocarpoxylon mazzonii has narrow, slightly demarcated growth rings. Each growth increment is characterized by a relatively wide zone of small, thick-walled cells in the earlywood followed by 6 to 11 thick-walled and tangentially-compressed cells in the latewood. The transition from earlywood to latewood is gradual.

The statistical tree ring analyses are summarized in Table 2. The mean ring width is 1.23mm; the mean minimum ring width is 1.11mm and the mean maximum ring width is 2.69mm. The width of the narrowest ring is 0.63mm and that of the widest is 3.62mm. The plots of selected growth-ring sequence are shown in Fig. 7. The growth rings are moderately wide and extremely uniform. These types are produced by trees that have grown under favourable and constant environmental conditions.

All of trees have wood with complacent ring, with Mean Sensitivity (MS) values between 0.09 and 0.29, an average value of 0.19. These data also indicate that the trees grew under favourable conditions in a uniform environment.

Annual Sensitivity (AS) values range from 0.051 to 0.725 (Table 2). These values indicate uniform climatic events. The histograms in Fig. 8 show very few variations in ring thickness from one year to the next, again reflecting favourable and constant environmental conditions.

Using CSDM curves, growth rings of the *Podocarpoxylon mazzonii* were further analyzed quantitatively. Four parameters were calculated: skew of CSDM curves, percentage of latewood, percentage of cell diminution in ring increment, and Ring Markedness Index (RMI) (Table 3 and 4). The CSDM curves for *Podocarpoxylon mazzonii* are right-skewed with a mean skew percentage of +40.23%, (range of +35.29% to +48.39%) (Fig. 9), implying that this species had an evergreen habit.

Measurements of percentage of latewood have traditionally been used to infer climatic conditions (Creber and Chaloner, 1984a, 1984b; Parrish and Spicer, 1988; Keller and Hendrix, 1997). However, the validity of this method has been questioned (Bailey and Faull, 1934; Larson, 1967; Chapman, 1994; Poole, 2000). Falcon-Lang (2000a, 2000b) pointed out that the degree of development of growth rings in conifer woods could be related to foliar retention, a genetically-determined characteristic. Falcon-Lang (2000a, 2005) has therefore recommended that the

TABLE 2 | **Summary of the growth-ring data for *Podocarpoxylon mazzonii***

Specimen number MPEF-Pb	Number of the rings	Mean ring width (mm)	Minimum ring width(mm)	Maximum ring width (mm)	Mean Sensitivity (MS)	Annual Sensitivity (AS)	
						Minimum values	Maximum values
Fossiliferous level I							
MPEF-Pb 2187 a	14	1.26	1.25	3.62	0.16	0.021	0.888
MPEF-Pb 2188 a	11	1.27	1.27	2.5	0.22	0.114	0.63
MPEF-Pb 2189 a	9	1.26	1.26	2.5	0.22	0.11	0.794
MPEF-Pb 2190 a	4	0.89	0.89	3.12	0.21	0.049	1.226
MPEF-Pb 2191 a	13	0.63	0.63	2.62	0.21	0.046	1.182
MPEF-Pb 2192 a	21	1.46	1.46	2.45	0.19	0.01	0.63
MPEF-Pb 2193 a	17	2.03	2.03	2.8	0.27	0.018	0.732
MPEF-Pb 2194 a	8	1.3	1.3	2.62	0.09	0.049	0.312
MPEF-Pb 2195 a	28	0.91	0.91	2.32	0.29	0.027	0.925
MPEF-Pb 2196 a	10	1.71	1.71	3.05	0.17	0.049	0.821
MPEF-Pb 2197 a	11	1.26	1.26	2.35	0.16	0.012	0.613
Fossiliferous level II							
MPEF-Pb 2198 a	12	1.15	0.75	2.07	0.28	0.095	0.727
MPEF-Pb 2199 a	7	1.17	1.25	2.5	0.09	0.072	0.373
MPEF-Pb 2200 a	4	0.89	0.75	3.12	0.21	0.049	1.226
Total	169						
Average		1.23	1.11	2.69	0.19	0.051	0.725

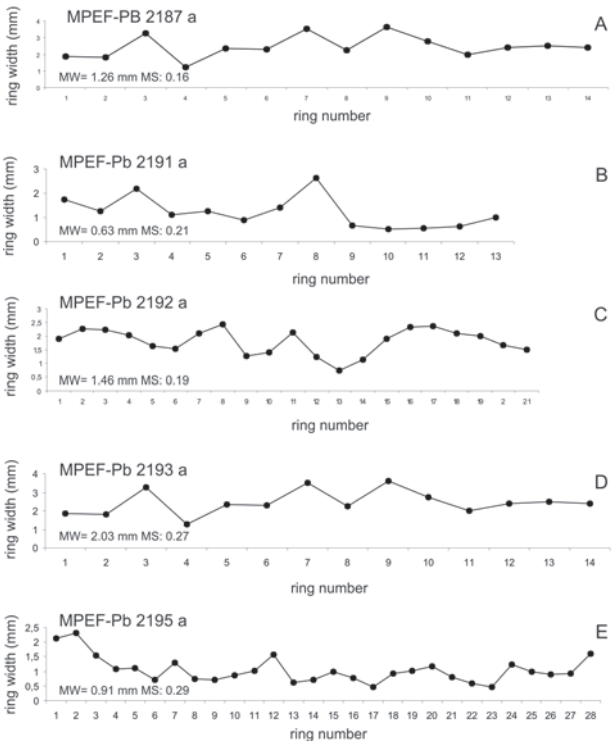

FIGURE 7 | **Graphs showing variation in growth-ring sequences of selected fossil tree of the *Podocarpoxylon mazzonii*. A) Specimen MPEF-Pb 2187, B) Specimen MPEF-Pb 2191, C) Specimen MPEF-Pb 2192, D) Specimen MPEF-Pb 2193, E) Specimen MPEF-Pb 2195. MW: mean width, MS: Mean Sensitivity.**

percentage of latewood should not be used as a climatic indicator because this characteristic may be strongly influenced by leaf longevity, in addition to reflecting intensity of climate seasonality.

The *Podocarpoxylon mazzonii* samples have latewood percentage ranges from 23.08%–35.29%, with a mean of 29.68%. The mean value of percentage of cell diminution in ring increment is 73.98% (68.75%–73.33%). Finally, the Ring Markedness Index (RMI) has a range of 15.85%–26.42%, with a mean of 22.03% (Fig. 8, Table 3).

These results indicate that the *Podocarpoxylon mazzonii* ring boundaries and ring increments are comparable to those of extant conifers with long Leaf Retention Times (LRTs) of between 2 and 6 years (Table 4). The subtle growth rings have tracheid diameters which increased across the growth increment and only decline in the last few cells.

COMPARISON WITH OTHER PALEOCENE FOSSIL FORESTS

There are other Paleocene petrified forests from the Salamanca Formation which are dominated by gymnosperms and with which the Ameghino Petrified Forest may be compared (Brea et al., 2005a, b). The Bororó Petrified Forest is located 200km west of the Ameghino Petrified Forest, near the Las Plumas Locality (Fig. 1). Although it contains a dominance of angiosperm trunks, it also contains fossils of the species *Podocarpoxylon mazzonii* (Petriella, 1972). Unfortunately, there is no published description of the growth ring from this locality which would allow further comparisons to be made. Two other Paleocene Patagonian fossil forests, known as the Víctor Szlápelis and Ormaechea Petrified Forests (45° 57' 31'' S - 69° 18' 49'' W and 45° 48' 53'' S - 69° 04' 01'' W respectively), are located 330km to the southwest of the Ameghino Petrified Forest, south of Musters and Colhué Huapi lakes. These two sites contain a dominance of gymnosperm trunks. The woods described from the Víctor Szlápelis Petrified Forest (Brea et al., 2005a) had growth-ring widths ranging from 1.31 to 6.03mm, with a mean width of 2.66mm. The maximum ring-width for any tree found south of 45° latitude is 11.30mm. The Mean Sensitivity (MS) ranges from 0.39 to 1.42, with an average

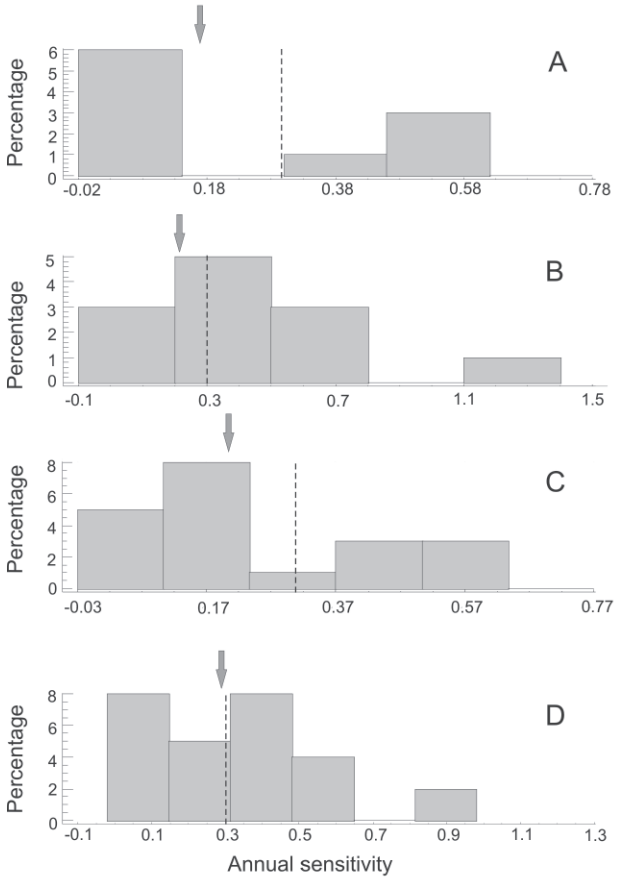

FIGURE 8 | **Histograms allowing comparison of variation in the annual sensitivities of selected fossil tree. The arrows indicate position of Mean Sensitivity (MS). Simple dotted line shows the MS: 0.30.**

TABLE 3 | **Results of the quantification of ring markedness parameters for *Podocarpoxylon mazzonii***

	Percentage latewood	Percentage diminution	Ring Markedness Index (RMI)	Percentage skew
ring 1	30.55	73.33	22.40	+38.89%
ring 2	35.29	72.22	25.49	+35.29%
ring 3	23.08	68.75	15.87	+30.77%
ring 4	29.03	68.75	19.96	+48.39%
ring 5	30.43	86.84	26.42	+47.83%
average	29.68	73.98	22.03	+40.23%

TABLE 4 | **Quantification of ring markedness parameters for the five extant taxa taken from data in Falcon-Lang (2000a, 2000b) (see the CSDM curves in Fig. 6). LRTs: Leaf Retention Times. The species highlighted in grey corresponds to the wood fossil studied in this paper**

	Species	Percentage latewood	Percentage diminution	Ring Markedness Index (RMI)	Range of percentage skew (mean value)
	Deciduous conifers				
	Larix decidua	50.00-54.83	71.55-85.91	35.77-44.36	-40.0 to +7.7 (-6.8)
	Evergreen conifers (LRTs in years)				
Increasing leaf longevity ↓	*Pinus sylvestris* (1-3 years)	41.03-50.00	70.53-77.28	31.56-35.26	-9.1 to +17.9 (+5.2)
	Picea abies (3-5 years)	25.93-44.19	74.02-84.03	19.90-35.42	0.0 to +38.2 (+12.0)
	Podocarpus totara (2-6 years)	---	---	---	+30.8 to +40.0 (+35.4)
	Podocarpoxylon mazzonii (? years)	23.08-35.29	68.75-86.84	15.87-26.42	+30.77 to +48.39 (+40.23)
	Cedrus libani (3-6 years)	30.77-39.58	62.33-72.06	20.22-24.68	+35.7 to +42.9 (+39.0)
	Araucaria araucana (3-15 years)	10.00-22.50	28.67-51.79	3.17-10.35	+55.0 to +80.0 (+66.7)

of 0.68 for all of the trees measured. The growth rings in the Ormaechea Petrified Forest, also known as the Sarmiento Petrified Forest (Brea et al., 2005b) had a mean average width of 2.10mm (0.28 to 6.59mm). The MS values are concentrated in a range of 0.34 to 0.95, with an average of 0.59. False rings were observed in many wood specimens from both of these fossiliferous localities. All samples have very narrow regions of latewood, consisting of only two to five small cells, indicating very rapid cessation of growth. The earlywood, however, is very well developed, indicating that the trees grew fast during the growing season in a very favourable environment. The presence of false rings and high MS values might reflect the fact that these trees grew near the forest borders as well as near the climatically-determined limits of their distribution. Tree rings analysis suggests that these trees grew under warm-temperate and humid climatic conditions, with dry summers and rainy springs (Brea et al., 2005a). The high MS (Mean Sensitivity) and AS (Annual Sensitivity) values in these forests indicate that the climate in that area was marked seasonal variation with extensive favourable growth periods and restricted unfavourable ones. The external factors that affected these cycles might be related to the location where the trees grew within the forest community.

The rings in the Paleocene woods from Bombala (Southern Monaro, Australia) described by Taylor et al. (1990) had a mean width of 0.97mm (0.96 to 1.31mm) and a mean MS of 0.28. These measurements reflect relatively narrow rings with low mean sensitivities, demonstrating the presence of climates that were markedly seasonal. The uniformity in ring width also suggests that conditions varied little from year to year. Furthermore, the narrow annual increments imply the presence of cool growing conditions in the southern highland of Australia during the Early Paleogene.

The growth ring analysis from the Ameghino Petrified Forest is consistent with the observations of Francis (1986) regarding Paleocene woods from Cross Valley (Seymour Island, Antarctica). The growth rings in these fossil woods are wide (0.52 to 5.70mm) and extremely uniform, with low MS values (0.228), suggesting that the trees grew in stable forest environments. The warm polar climate interpreted using Paleocene macroflora (Francis, 1986) is consistent with an increase in the global atmospheric carbon dioxide levels for this stage (Beerling and Jolley, 1998).

DISCUSSION AND CONCLUDING REMARKS

Sedimentological data from the Ameghino Petrified Forest suggest that the paleoenvironments in the Salamanca Formation varied from a sandy fluvial system to estuarine and wave-dominated tidal plains. This type of coastal environment is characterized by surf and a sequence of shoreface types that are heavily bioturbated. In the lower section of the unit, well-preserved plant remains with a low degree of disarticulation were preserved in very coarse facies of the estuarine environment (FL I) as well as in heterolithic facies of the shoreface environment (FL II). This indicates a low-energy paleoenvironment, with plants found in close

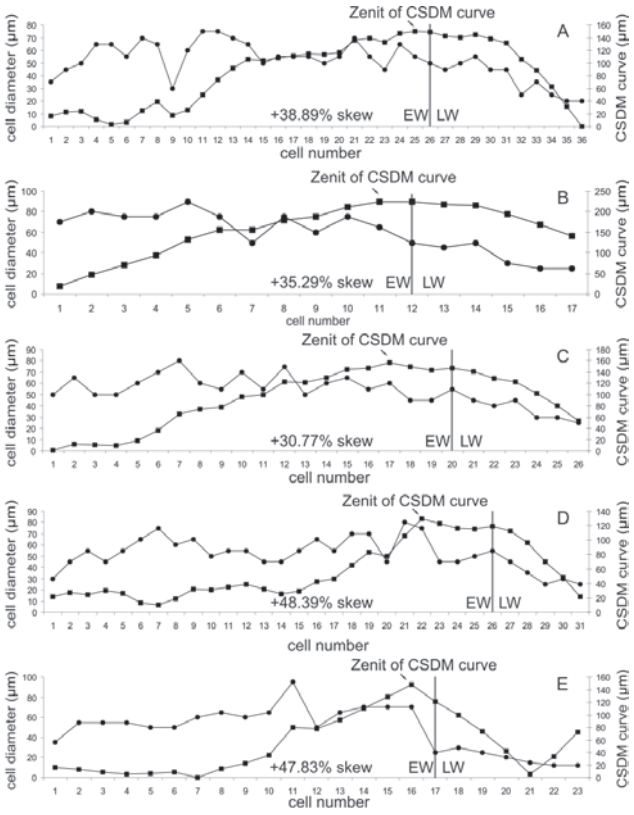

FIGURE 9 | **Right-skewed CSDM curves of five growth rings and cell diameters of growth ring increment. For each ring increment, the percentage of skew for CSDM curves was calculated using Falcon-Lang method (2000a). The distance where CSDM curve reaches the zenith represents the percentage of skew in relation with the total distance between the centre of the CSDM curve to the right of the plot.**

proximity to the site where the plants grew. Towards the top of this section, intertidal channels can be observed and indicate more energetic paleoenvironmental conditions. The calcareous deposits in the upper section represent coastal bars which were intensely bioturbated by *Glossifungites* icnofacies, and these lack preserved plant remains.

Evidence including the presence of palm leaves, the coriaceous texture of wood dicotyledonous leaves, the results of growth-ring analyses, and the presence of limestones all support interpretation of a warm-temperate climate during this epoch.

Early Paleocene floras from the Ameghino Petrified Forest are dominated by podocarpaceous gymnosperms, with all permineralized woods specimens assigned to a single species, *Podocarpoxylon mazzonii*. These podocarpaceous conifers have a mean estimated original diameter (D_{est}) of 40.11cm (89.13–25.46cm) and a mean estimated height (H_{est}) of 20.07m (16.80–28.80m).

The presence of well-defined growth rings during the Early Paleocene epoch demonstrates that tree growth was controlled by well-defined seasons. The narrow late wood may be attributable to inherent genetic characteristics of the tree.

Mean Sensitivity (MS) values indicate that the fossil woods had rings which were uniform in width from year to year. Histograms created for Annual Sensitivity (AS) values for each tree also indicate that variation in growth was very low, with most of the values being less than 0.3.

Fossil tree ring analysis indicates trees growth in a favourable and uniform environment, growing seasons that ended abruptly, and an absence of frosts and droughts. The uniform width of the rings is the most revealing signal, since modern trees with similarly low MS values are found in stable forest environments where no single limiting factor exists. This type of growth is correlated with trees which grow in forest interiors (Fritts et al., 1965; Francis, 1986). This type of growth is also a feature of extensive and dense forests (Taylor et al., 1990), an interpretation that is also supported by the preservation and orientation of the logs.

Quantitative growth-ring analysis can be used to hypothesize that *Podocarpoxylon mazzonii* was an evergreen gymnosperm.

Our results indicate that the Ameghino Petrified Forest was dominated by monotypic evergreen podocarps that reached a height of 20m, which grew in a dense forest and developed in a uniform warm-temperate climate.

Early Paleocene megafloral assemblages from Central Patagonian mid-latitude locations demonstrate the existence of forests dominated by evergreen conifers, mostly of the Podocarpaceae, which developed under warm-temperate climatic conditions. Such forests were widely distributed in Patagonia during the Early Paleocene (Petriella, 1972; Brea et al., 2005a, 2005b). Evidence indicates that these climatic conditions persisted mid-latitude South America throughout the Danian (Salamanca Formation) and across the Danian-Selandian boundary (Peñas Coloradas and Las Flores Formations) (Raigemborn et al., 2009).

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